

FIGS. 1-4. In FIGURES 1 to 3 the dimensions and form of the components of these composite drawings were obtained from camera lucida drawings and electron micrographs. Magnification, as reproduced $\times \frac{1}{2}$, ca. 1,100. 1, *Degeneria vitiensis* microspore prior to microspore mitosis. Cross section through the unexpanded aperture. 2, Cross section through mature pollen of *Degeneria*. 3, Longitudinal medial section through aperture of mature pollen of *Degeneria*. 4, Camera lucida drawing of whole mount of a *Degeneria* pollen grain with the distal pole uppermost showing margin of the aperture. Magnification, $\times \frac{1}{2}$, ca. 750.

There was an intine-like, low density layer 0.4 to 0.05 μ in thickness under the nonapertural exine. At the aperture, the intine-like material took the form of a thick, lens-shaped layer which showed localized dense channels or pockets of material (FIG. 8). This layer was rapidly and differentially stained with ruthenium red precisely as was the case in the apertural intine of the mature pollen grains.

In addition to the well defined exine and a translucent intine-like layer

there were several dense lamellae between the exine and the presumed intine (FIGS. 6 & 9).

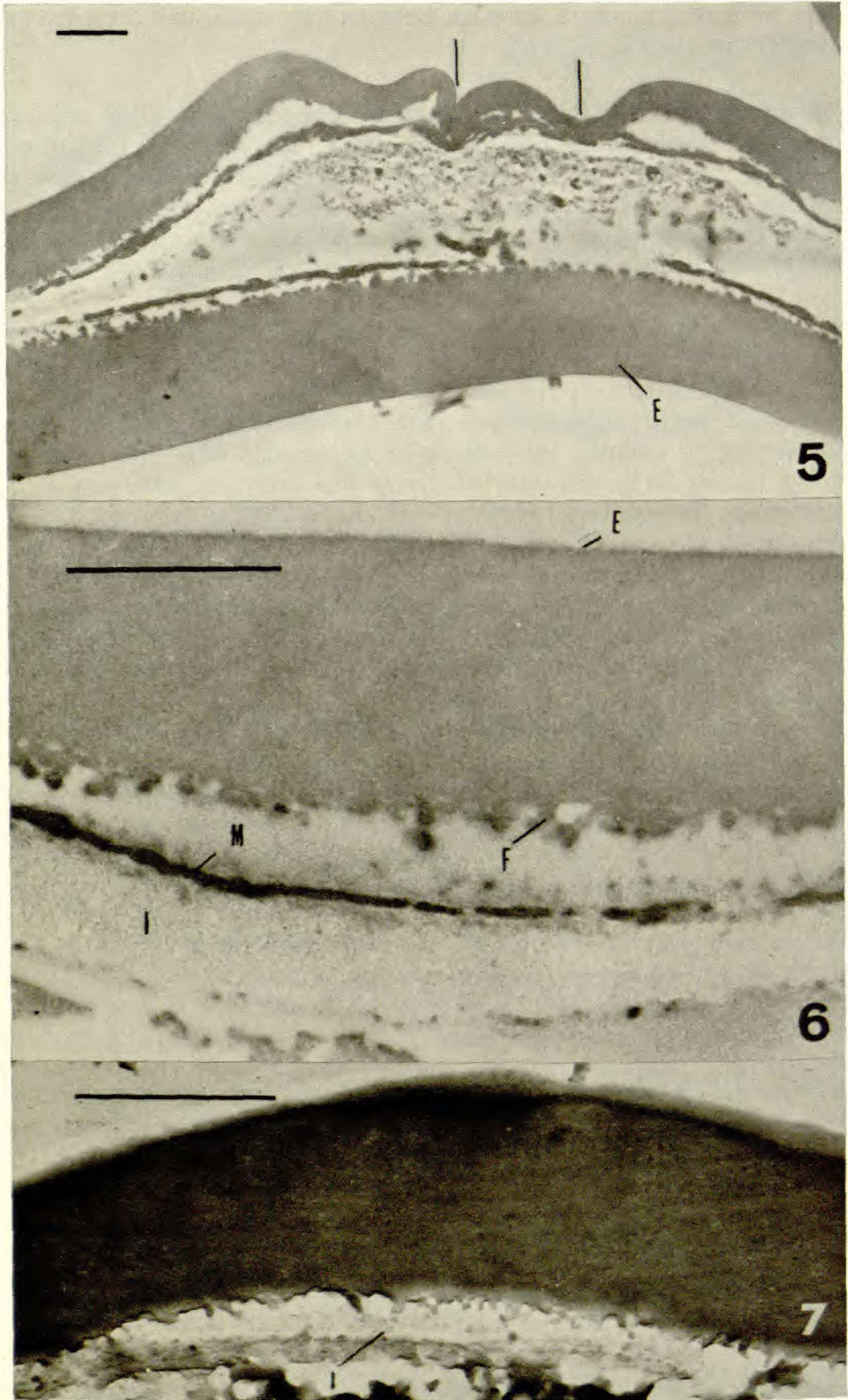
Mature Pollen Grain. The germinal aperture formed the only differentiated feature of the psilate pollen grain. The aperture extended over the distal surface to a point below the equator. At the distal pole, the aperture was usually constricted while its ends were enlarged (FIG. 4). A distinct but irregular exine margin was visible at an upper focal level with phase contrast microscopy. At a lower focal plane, a well delimited layer broader than the exinous opening ran the length of the furrow. This was made conspicuous with the ruthenium red reagent. In surface view, the layer appeared foveate, whereas in optical section it presented a columellate or striate appearance (FIGS. 10 & 11).

The aperture of pollen treated with Novopokrowsky's chloriodide of zinc for ca. 30 minutes was striking in its greenish color and clearly revealed in the Zwischenkörper relatively fine structure having a striate appearance. In equatorial views of such pollen grains, the generative cell was usually close to the proximal pole, whereas the tube nucleus, while adjacent, was closer to the distal pole. The generative cell is about 12 μ in diameter with a nucleus 6.7 μ in diameter and a relatively inconspicuous nucleolus approximately 1.6 μ in diameter. In contrast, the tube nucleus is approximately 10 μ in diameter having a relatively conspicuous nucleolus some 5 μ in diameter.

We obtained positive reactions for cellulose in a thin layer bounding the protoplast but with the available specimens the microchemical tests were frequently imprecise and difficult to interpret. With Novopokrowsky's iodine-zinc chloride treatment a greenish coloration appeared, while a slight bluish-green reaction occurred in the intine when iodine-potassium iodide followed by 65% sulphuric acid were used. After bleaching with 30% H₂O₂ some of the pollen grains badly darkened by long storage in fixative gave, with the IKI-H₂SO₄ procedure, a purplish reaction possibly suggestive of cellulose at the surface of the protoplast. In unfixed pollen of *Liriodendron*, these procedures resulted in the typical blue cellulosic reaction in the inner intine of many grains. Bailey (1960), Martens and Waterkeyn (1962), et al. have reported the characteristic presence of cellulose in inner intine in a wide range of taxa including Magnolian and Ranalian species. Final decision on its occurrence in *Degeneria* can best be made with additional observations on fresh material.

In electron micrographs of pollen stained with osmium tetroxide and embedded in methacrylate, the intine was seen to be composed of two zones (FIGS. 2 & 15). The inner zone was comparatively uniform in texture. Near the terminus of the aperture this zone had an internal thickening or bulge (FIGS. 12 & 15). In nonapertural regions, the outer zone consisted of strands which graded into material of spongy appearance in the apertural part of the pollen grain (FIG. 15).

The appearance of the intine of pollen grains embedded in "Vestopal" following staining with osmium tetroxide, uranyl acetate or potassium



permanganate differed from the above in lacking a stranded inner zone (FIGS. 14 & 17). Analysis of sections before and after removal of embedding matrix and shadowing showed that the spongy part of the intine was composed of ramifying channels within the outer subdivision of the intine (FIGS. 15 & 16). In sections, the channels contained a dense substance (FIG. 17). Such channels were also visible in electron micrographs and phase contrast photomicrographs of the germinal aperture in *Liriodendron* pollen fixed in osmium tetroxide or potassium permanganate (FIGS. 18–21).

In the early formation of the apertural intine of *Liriodendron*, strands of microspore cytoplasm penetrated directly into the spongy structure (FIG. 18). Elements of the endoplasmic reticulum were seen to extend into the channels (FIG. 19). The inner zone of the intine was introduced at a later stage of development (FIGS. 20 & 21).

During maturation of the aperture in the pollen grain, cytoplasmic strands crossed the inner zone of the apertural intine and connected with the substance in the channels of the outer zone (FIGS. 20 & 21). When *Liriodendron* pollen reached maturity the channels still contained dense material, but connections with the cytoplasm through the inner part of the intine did not persist. Sections of *Liriodendron*, used for phase contrast microscopy, showed continuity of the material within channels of the intine and the cytoplasm (FIG. 13).

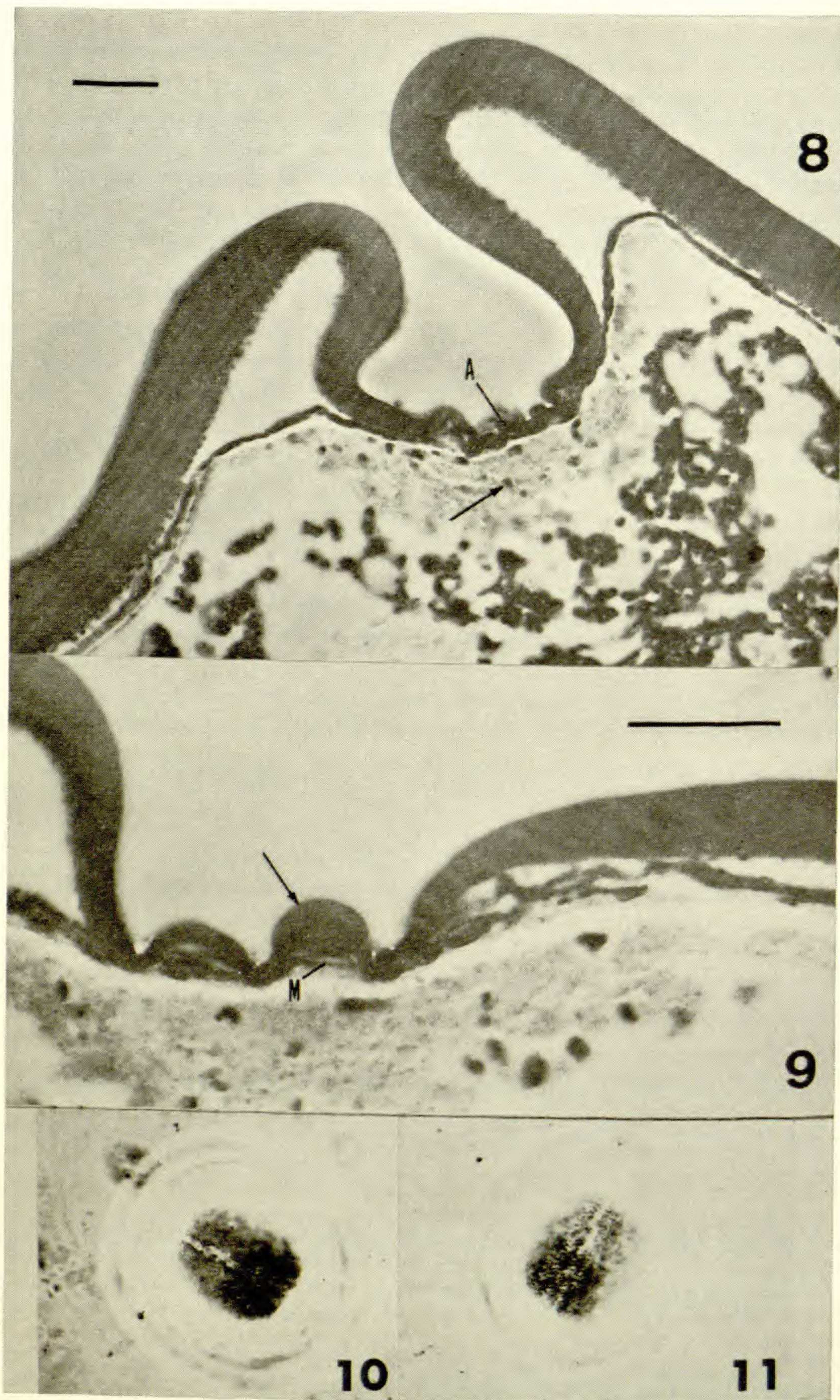
In sections of *Degeneria* anthers, small round bodies (0.44 to 0.55 μ in diameter) having a density the same as the exine, some with an eccentric cavity, were seen between the locule wall and the pollen wall (FIG. 15).

DISCUSSION

In its complex of pollen characters, *Degeneria* has natural alliance with Magnolian taxa (Bailey and Smith, 1942; Swamy, 1949). The single distal aperture is a familiar basic character. The following distinguishing characters were observed in pollen of *Degeneria*: a narrow furrow extending over the distal hemisphere and ending somewhat below the equator in

(NOTE: beginning with FIGURE 5, the black scale line on the electron micrographs is equal to one micron.)

FIGS. 5–7. 5, Electron micrograph of *Degeneria vitiensis* microspore fixed in Fiji by histological methods. Exine tapering gradually in thickness toward differentiated but unexpanded apertural region (between lines). Microspore is collapsed so a portion of exine of proximal surface (E) is near aperture. Exine of proximal surface may be 15 times thickness of exine of apertural region. Magnification ca. 9,000. 6, Electron micrograph of nonapertural exine of a *Degeneria* microspore. Outer surface of exine (E) smooth, inner surface (F) fimbriate; dense material (M) of a seemingly laminate nature between exine and intine (I), remnant of cytoplasm below the intine. Magnification ca. 28,000. 7, Section of *Degeneria* pollen exine similar to FIGURE 6, but with embedding material removed and section shadowed with chromium. Fimbriae of inner surface of exine seen against intine (I) which has become separated from exine. Magnification ca. 26,000.

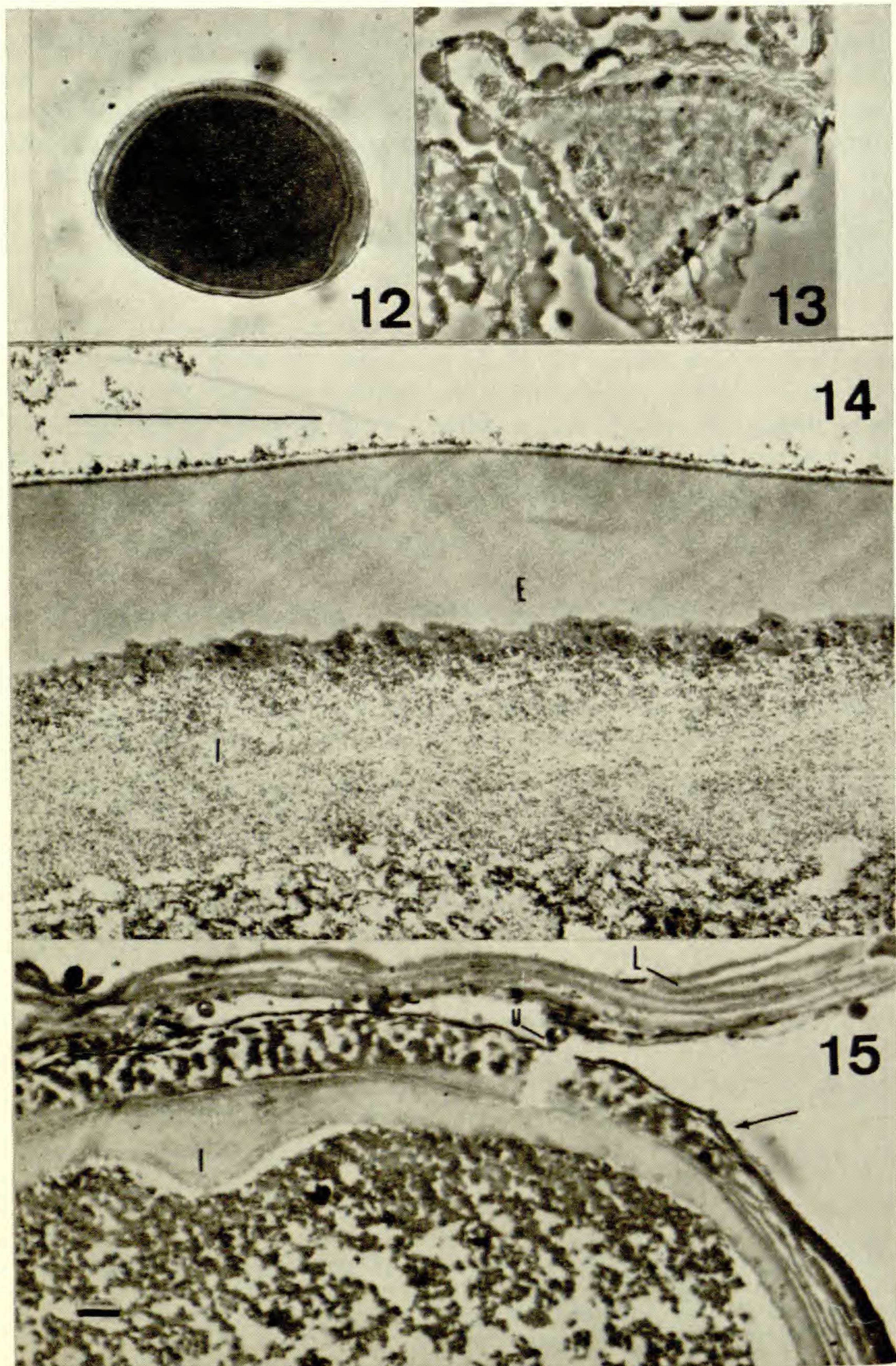


FIGS. 8-11. 8, Electron micrograph of *Degeneria* microspore. Exine at

the proximal hemisphere; a dumbbell-shaped aperture caused by an increase in the width of the furrow in the equatorial region; an extremely thin exine covering the distal surface with the exception of the narrow aperture; and a smooth and internally amorphous exine even at magnifications of the order of 30,000 times. Many pollen types described as psilate are found to be ornamented as improved methods of observation can be applied, but *Degeneria* offers an example of an exine that is truly psilate.

The remarkable sponge-like apertural structure (*Zwischenkörper*, Fritzsche, 1837) of *Degeneria* pollen is portrayed in the electron micrographs used for FIGURES 15, 16, and 17. The channeled *Zwischenkörper* of *Degeneria* microspores and pollen grains is similar to apertural structures observed in *Liriodendron tulipifera* (FIG. 20). In *Liriodendron* preparations it is clear that the channels which are isolated in the *Zwischenkörper* in mature pollen were part of a system of cytoplasmic strands connecting the wall with peripheral cytoplasm of the microspore during early stages of development (FIGS. 13 & 18). As in *Liriodendron*, the *Zwischenkörper* of *Degeneria* was quickly responsive to specific ruthenium red staining. In microspores and mature pollen of both genera the ruthenium red reagent sharply differentiated the *Zwischenkörper* as a channeled ribbon-like structure. The red-violet ruthenium red coloration usually first appeared in equatorial regions of the germinal furrow, and the color was deeper there than in the distal region. Presumably, areas of intense coloration following ruthenium red staining were loci of high polyuronide concentrations (Bailey, 1960) and were related to the system of cytoplasmic strands. In Dr. A. C. Smith's collection No. 5880 we found grains with pollen tubes in various stages of emergence. Pollen tubes were also reported for this material by Swamy (1949). The pollen tubes we saw had gained exit at the ends of the germinal furrow in the region giving the most intense reaction to ruthenium red. The exine bounding the apertural area tapered to a thinness of 10–50 millimicra over the *Zwischenkörper* (FIG. 15) and was difficult to separate from the *Zwischenkörper* in our electron micrographs (FIG. 16). Evidence for an exine-like covering over the distal surface comes from LO analysis of intact pollen and the resistance of material in that part of the wall to acetolysis. In mature grains stained with potassium permanganate, the exine seemed to

presumptive aperture (A) is differentiated into a thin and folded form, but there is no opening; intine is lens shaped in apertural region and considerably thicker than elsewhere; localized pockets of dense material (arrow) may be seen in intine. Magnification ca. 11,000. 9, Similar to FIGURE 8 except for thickening (arrow) which is part of folded preapertural exine (thickenings of this nature seen at aperture margin in mature pollen). Dense lamellae (M) may be seen between exine and intine. Magnification ca. 20,000. 10, *Degeneria* (Smith 5744), FAA fixation; chloral hydrate mounting medium; phase contrast; upper focal plane at level of apertural margin. Lens-shaped *Zwischenkörper* appearing foveate in surface view and striate in optical section. Magnification ca. 1,400. 11, Same pollen grain as in FIGURE 10, except lower focal plane at level of channeled *Zwischenkörper*; phase contrast. Magnification ca. 1,400.



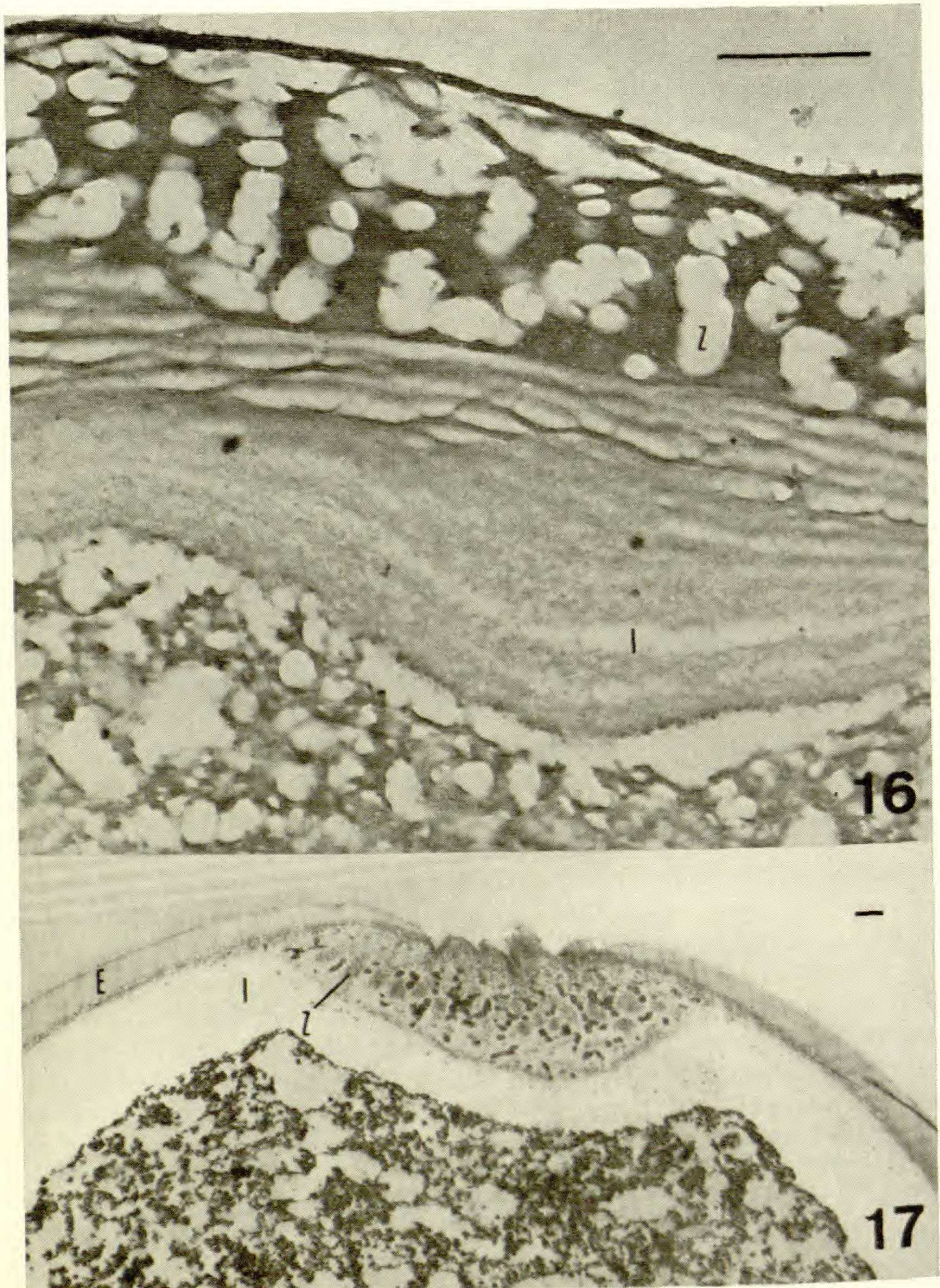
FIGS. 12-15. 12, *Degeneria* (Smith 5744), FAA fixation; lactic acid mounting medium; without phase contrast; optical, almost median, section of distal aperture. Magnification ca. 1,400. 13, *Liriodendron tulipifera* (Univ. of Minnesota Bot. Garden); fixation 57 (6-8)-22 RS #4; ultra thin section mounted

terminate near the limits of the Zwischenkörper while the dense material between the exine and intine continued out over the intine. The lateral extent of the apertural area and Zwischenkörper is not apparent in FIGURE 17 because the aperture is not fully expanded, but the figure illustrates the above relationships of the homogeneous exine, intine, and dense middle material.

Exclusive of the thin exine-like material over the Zwischenkörper, the area of the exine is only slightly greater for mature pollen than for microspores. Accommodation for the increased surface area demanded by the greater volume of the protoplast of mature pollen, as shown in FIGURES 1 and 2, seems to reside in the thin cover over the Zwischenkörper and the expanded ends of the aperture. The thin exinous covering of the apertural region must originate either by stretching of existing exine (perhaps the folded covering seen in presumptive apertures of microspores in FIGURE 8) or by proliferation from new sporopollenin between the microspore and mature pollen stages.

For *Degeneria* there is little evidence for deciding between the alternatives, stretching of existing exine or deposition of new sporopollenin. The fimbriae of the inner exine surface change slightly in form from the microspore stage to mature pollen (Figs. 6 & 14), tending to be more widely spaced and shorter in the mature exine. This phenomenon could be used with equal justification to argue for expansion of the entire exine cover or addition of new sporopollenin. Addition of at least some new sporopollenin to the exine following attainment of exine final form, prior to microspore mitosis, was reported for pollen of *Poa annua* (Rowley, 1962). But evidence is also available to support modifications in exine form by expansion of the exine. Kuprianova (1948) proposed that the differences in pollen size and shape in the Commelinaceae were largely the product of variation in the amount of expansion of the apertural part of the grains. In mature grains of *Polia*, *Floscopa*, and *Commelina*, Kuprianova's illustrations suggest expansion of apertural ornamentations from a system like the nonapertural part of these pollen grains. In *Commelinantia anomala*, where conditions for determining the stage of development and fixation were more satisfactory than for *Degeneria*, we have made some deductions

in 1:1 poppyseed oil-butanol; phase contrast. Lines in intine perpendicular to pollen protoplast are channels containing cytoplasm. Magnification ca. 1,800. 14, Electron micrograph of nonapertural part of mature exine of *Degeneria* pollen. A zone of dense material is between the exine (E) and intine (I); outer surface of exine is smooth, inner surface undulate to fimbriate. Fimbriae of mature exine less closely spaced than at microspore stage (cf. FIGURES 6 and 7). Magnification ca. 31,000. 15, Electron micrograph of section made perpendicular to aperture in mature *Degeneria* pollen grain. Exine tapering to thinness of 10 to 50 millimicra over aperture (arrow indicates right margin of aperture), intine with two zones, the inner comparatively uniform but with internal thickening (I) oriented parallel with aperture in the equatorial region; the outer part of intine constructed of strands (lower right) which join the spongy material at aperture margin; small round bodies (U), some with central cavity, located between locule wall (L) and pollen grain. Magnification ca. 5,000.



FIGS. 16 and 17. 16, *Degeneria*, the same material as in FIGURE 15 following removal of the methacrylate and shadowing with palladium. Internal thickening of inner part of intine at the lower right (I); spongy intine subdivision (Z), over inner intine, is composed of ramifying channels. If there is an exinous covering it must be on the order of 10 millimicra in thickness. Magnification ca. 18,000. 17, Electron micrograph of section of mature *Degeneria* grain cut across narrow part of aperture, at distal pole. In this KMnO_4 -stained material, dense material between exine (E) and intine (I) extends out over the *Zwischenkörper* (Z). Channels in *Zwischenkörper* contain dense substance. Magnification ca. 3,500.

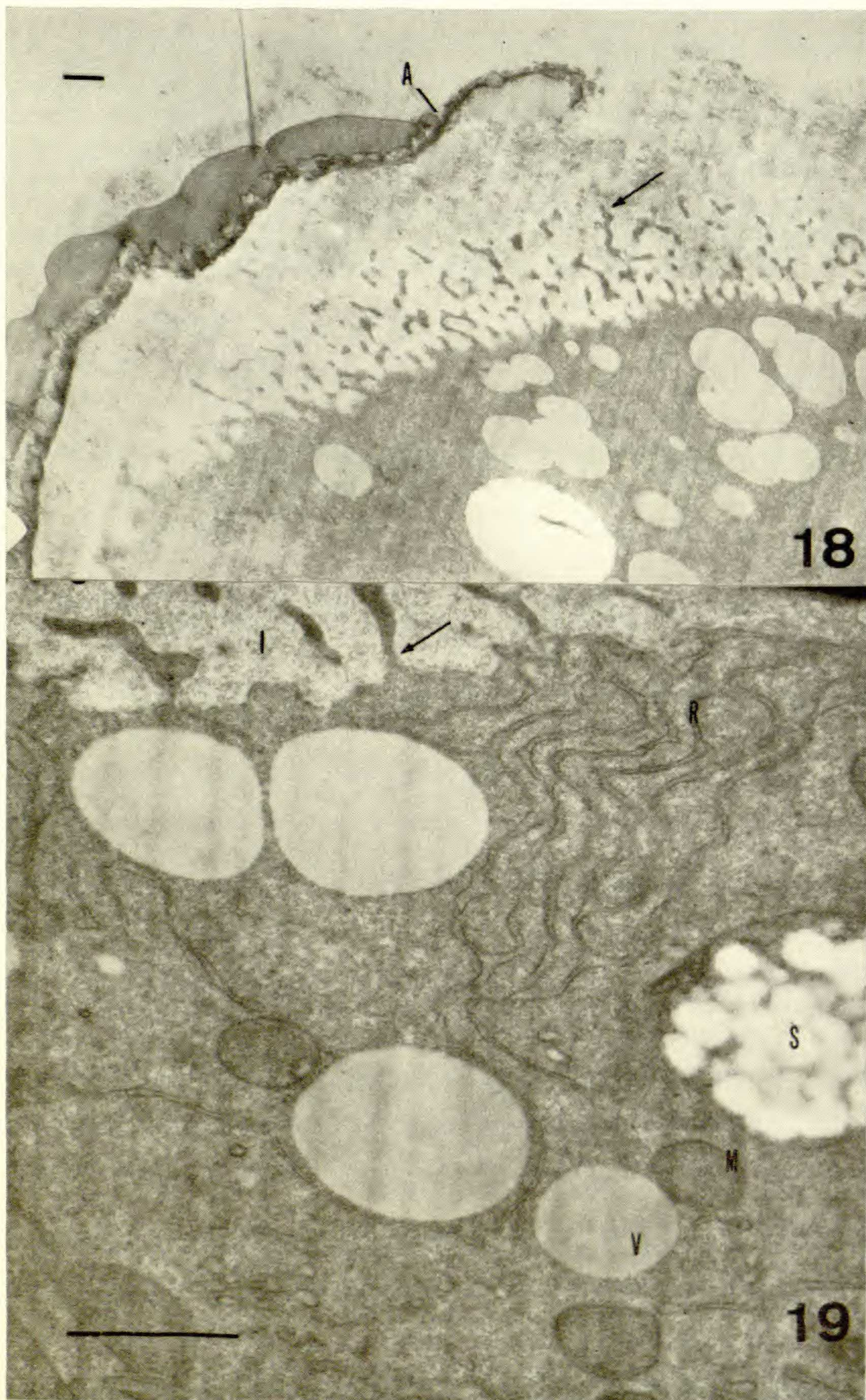
which parallel Kuprianova's suggestions and may be partially applicable to formation of the thin exine bordering the *Degeneria* aperture (Rowley & Dahl, 1962). In *C. anomala*, insulae bisected by the aperture margin had the appearance of apertural insulae at one end and nonapertural insulae at the other with indications of deformation by stretching in the middle regions. The endexine was reduced in height in the middle region from about 500 to 50 millimicra, concomitantly going from a sheet to a network, and the tegillar ends of columellae were tilted toward the aperture. We feel that these effects could be produced by movement of the apertural ends of insulae bisected by the aperture margin toward the aperture. The proximal ends of columellae around the periphery of apertural insulae splay outward and augment the notion that tension could be responsible for the tilting of columellae and conversion of endexine from a sheet to net form.

It may seem self evident that new sporopollenin would be added throughout the period of exine enlargement, but there are observations which suggest that the addition of new exine material is either stopped or does not keep pace with the area increase required by volume changes in the pollen protoplast during final maturation. In work with pollen of the Amaranthaceae Kajale (1940), for example, noted that the exine in mature grains was thinner than in earlier stages apparently due to its being stretched by protoplast growth.

Round bodies were seen in *Degeneria* anthers between the tapetum or locular wall and the male gametophyte in quartet, microspore, and mature pollen stages. These bodies frequently had central or eccentric openings of low density which in mature stages were found to be empty cavities after removal of the embedding material and shadowing with heavy metals. These exine-like bodies are similar to the tapetal secretion droplets, orbicules, or Ubisch bodies described or reviewed by Maheshwari (1950), Erdtman, et al. (1961), Heslop-Harrison (1962), Takats (1962), and Rowley (1963). In *Degeneria*, these orbicule-like bodies exhibit the psilate surfaces characteristic of the mature exine. It appears possible that some association exists between orbicules and the mature exine in the character of the ornamentation of the respective surfaces.

SUMMARY

Based upon material fixed by Dr. A. C. Smith in Fiji, the mature pollen wall of *Degeneria vitiensis* I. W. Bailey & A. C. Smith is psilate and tapers gradually from the proximal surface to a thin edge in the apertural region. The exine is internally amorphous. The inner surface is not smooth like the outer but fimbriate. The intine is subdivided into an extensive lens-shaped Zwischenkörper, an outer part limited to the apertural region, and an inner part that envelops the cytoplasm and has but one distinguishing feature, a longitudinally oriented bulge parallel with the aperture and protruding into the cytoplasm. Ramifying channels in the Zwischenkörper contain a dense material. Several photomicrographs and electron micro-



FIGS. 18 and 19. 18, Electron micrograph of *Liriodendron tulipifera* micro-

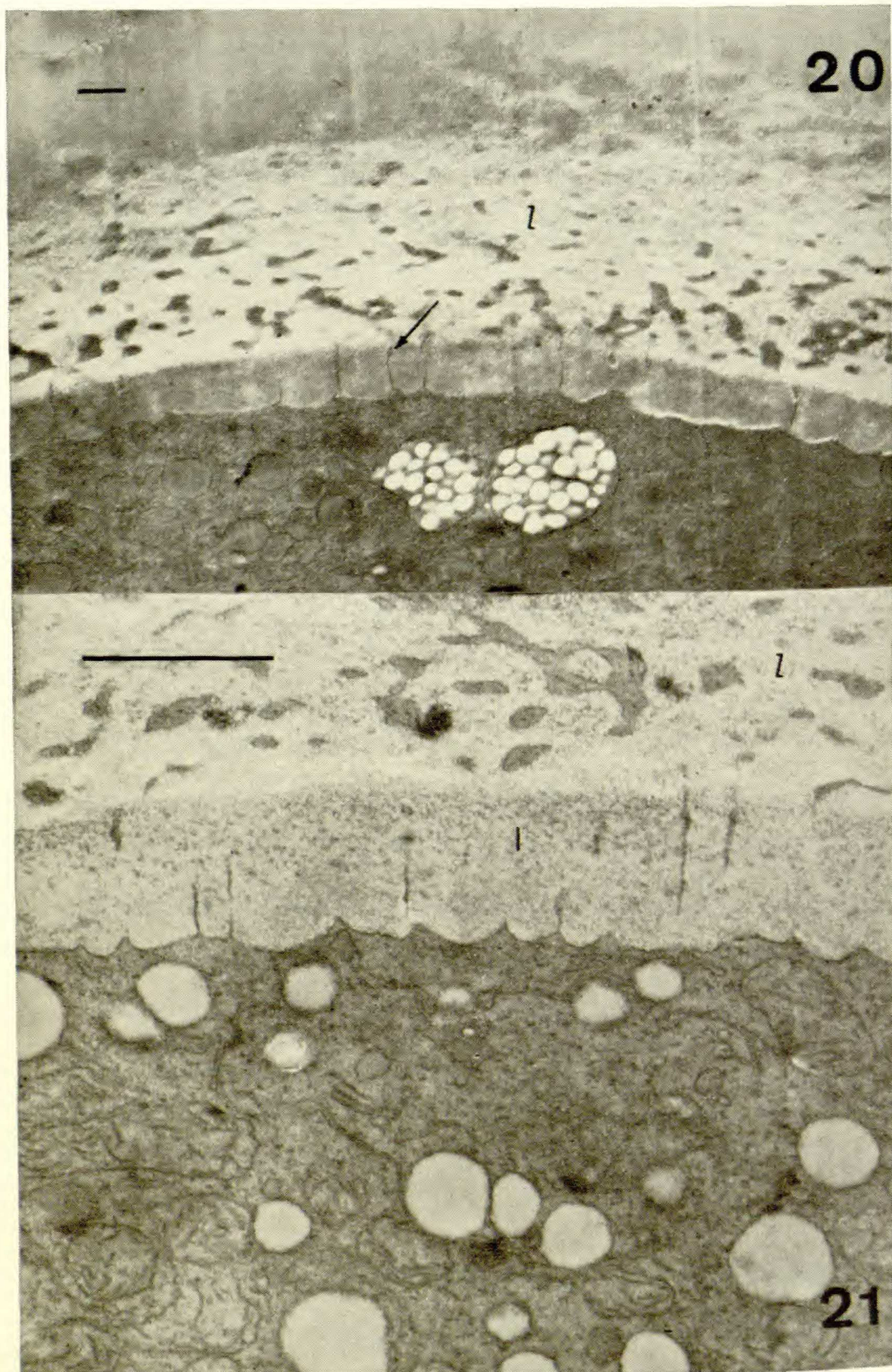
graphs of pollen of *Liriodendron tulipifera* are included to demonstrate continuity of the dense material in the Zwischenkörper with the pollen cytoplasm in that species.

Quartet and late microspore stages are compared with mature pollen grains of *Degeneria* to suggest the mode of aperture differentiation and sequence of formation of the intine subdivisions. A dense material was seen between the homogeneous exine and the intine in both late microspores and mature pollen. Round exine-like bodies seen between the wall of the pollen grain and the tapetum or locule wall may be orbicules.

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spore fixed in KMnO_4 and embedded in "Vestopal-W." Intine greatly thickened in region of aperture (aperture margin, A); early localization of cytoplasmic strands near protoplast occurred, although dense inner part of intine forms following microspore mitosis (see FIGURE 20). Magnification ca. 5,000. 19, Electron micrograph of *L. tulipifera* microspore at stage similar to material in FIGURE 18. Detail of junction between intine (I) and microspore cytoplasm; elements of endoplasmic reticulum (R) passing into cytoplasmic strands of intine (arrow); labeled cytoplasmic organelles are mitochondrion (M), vacuole (V), and starch grains (S) in a plastid. Magnification ca. 22,000.



FIGS. 20 and 21. 20, Electron micrograph of nearly mature pollen of *Liriodendron tulipifera*. Thick section showing cytoplasmic connections across inner part of intine (arrow) with cytoplasmic areas in the *Zwischenkörper* (Z). An inner zone of greater density to electrons developing in the intine near maturity

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of the pollen grain. Magnification ca. 6,000. 21, Electron micrograph from a thin section of the grain shown in FIGURE 20. Figure includes some of tube nucleus cytoplasm at bottom, dense inner part of intine across center (I), and part of outer portion of intine of the aperture at top (Z). Magnification ca. 24,000.

LETTERS FROM CHARLES SPRAGUE SARGENT TO
REGINALD SOMERS COCKS, 1908-1926 *

Edited by JOSEPH EWAN

147

June 26, 1917.

It is a long time since I have had any word from you. I hope you have not, like most of the rest of the world, given yourself up to raising potatoes and cabbages. There is too much botany left to be finished in Louisiana for that. I shall be glad to hear what you have seen and accomplished since you last wrote.

148

June 29, 1917.

The enclosed memorandum,¹³ which do not return, may be of service to you.

I do not understand why we overlooked this tree when we were at Hammond, but I suppose we were busy thinking of other things.

How about the small Live Oak which we saw there on the prairies? I hope you won't fail to get the fruit.

149

July 18, 1917.

It is such a long time since I have had any word from you that I am beginning to be anxious about you. I hope you are not sick or otherwise incapacitated. Won't you drop me a line?

150

August 22, 1917.

Glad to get your letter even if it is written from such a place as Berlin.¹⁴ I am glad that you will undertake the Opelousas and Springfield Oaks and I am counting on you to do this. I hope you will get specimens of the Oak with rhomboidal leaves.

You say that I have flowers of the Lake Charles Linden, but I haven't flowers, only young buds, of the Linden of which I need material, that is the tree at the ferry in West Lake Charles. If you have ever collected flowers of this I hope you will let me have them. This you know is the tree which has puzzled us a good deal and which we thought last spring was different from any of the other Louisiana Lindens.

* Continued from volume 46, p. 159.

¹³ Enclosure missing.

¹⁴ 2 mi. s. of Sardis, Dallas Co., Alabama.

Is there any chance of your being north this summer?

P.S. — Do you remember that *Carya alba*-like tree by roadside near Loring with slender branchlets and very tomentose young leaves? I judge that the Winnfield tree which has so long bothered us is the same and I have specimens of what I take to be the same thing from Natchez. This is a tree which needs investigation. It may be only a variety of *alba* but it is unusual and we need mature leaves and fruit.

151

August 27, 1917.

I have yours of the 23rd and the specimen of *Quercus*, for which many thanks. This is not a straight *rhombifolia* but may be a form of it with lobed leaves. Notice the long-stalked fruit. I hope you will get specimens later and if possible find more trees.

There are no end of forms apparently of these southern Oaks. What should you think of the proposition of referring everything from Louisiana which has been called *laurifolia* to forms of *Q. nigra*?

152

October 27, 1917.

I am delighted with your bundle of specimens. The leaves of *Quercus geminata* are much thicker and more prominently veined than those of *Q. virginiana*. The Louisiana Live Oak is like the type as known to Catesby, Linnaeus, etc.

Quercus geminata, which is described as a small tree, by Small, is at Biloxi a large tree, as large as the common Live Oak with which it grows. It often has solitary fruit just as the typical Live Oak has the fruit in pairs, in threes or in fours in spite of anything Sargent's Manual may say. *Quercus virginiana* and *Q. geminata* seem to run together and I am going to consider the latter a form of the former. Small and Britton evidently got the two a good deal mixed up. I have not seen *Quercus geminata* from Louisiana or Texas.

We have no specimens of *Q. myrtifolia* from Louisiana and it should be dropped from the state unless we can get some real evidence of its occurrence there. The Chandeleur Islands are where it might be expected. Do you know anything of these Islands? I regret to say that we have no specimen from the Islands in Mississippi Sound on which this plant is reported to be very common. How can one be obtained?

Is your *Quercus* No. 4334 from Opelousas one of the trees with scaly bark in the low ground near Washington? This number seems to be the only one which has fruit. It may be hard to distinguish this specifically from the Post Oak, but it is evidently a distinct variety and a very fine tree.

Quercus No. 4716 near Hammond, Sargent and Cocks, in the spring. Is this from the small tree on the prairies with pale bark and slender drooping branches? If so, it seems to be an undescribed and interesting form of the Live Oak. Your small shrubs seem to be the same, so I suppose it is both a tree and a shrub.